THE IDENTITY OF *HELICARION SEMONI* MARTENS, 1894: A LARGE SEMI-SLUG FROM THE WET TROPICS, NORTHEASTERN QUEENSLAND (PULMONATA: HELICARIONIDAE)

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The identity of the semi-slug *Helicarion semoni* Martens, 1894, is established. The name is applied to a large species from the northern region of the Wet Tropics, NEQ, and the type locality is redesignated as the Big Tableland, south of Cooktown, NEQ. On the basis of conchological and anatomical features the species is referred to *Thularion* gen.nov. and redescribed. Some aspects of its biogeography and relationships are discussed. □ *Pulmonata, Helicarionidae, Thularion semoni (Martens, 1894), new genus, semi-slug, systematics, biogeography, Wet Tropics.*

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Semi-slugs belonging to the family Helicarionidae are particularly diverse in eastern Queensland. Iredale (1937) listed 8 species while Smith (1992) listed 7 with a further 2 as incertae sedis. Based on material acquired by the Queensland Museum over the past 13 years these are underestimations. Among the described forms several, including *Helicarion semoni* Martens, 1894, are taxonomic enigmas. Although listed under *Parmacochlea* Smith, 1884, by Iredale (1937) the species was considered incertae sedis by Smith (1992). Long efforts by the author to locate the type were fruitless until a chance discovery of two syntypes by Dr Rudolf Kilias in the collections of the Zoological Museum, Humboldt University, Berlin. Examination of the types revealed that they were conspecific with a large helicarionid semi-slug from the northern region of the Wet Tropics, NEQ.

The type locality given by Martens (1894) was Burnett R., SEQ (Fig. 1), which may explain the confusion surrounding this species even though the original descriptions of both shell and animal were excellent. Marten's introduction of *H. semoni* was included in a listing of molluscan species (land and freshwater) collected from eastern Queensland in 1891-1893. Although the Burnett R. featured in several species descriptions other Queensland localities were visited by the expedition and these included Hammond Is., Torres Strait, and Cooktown, NEQ. Since both the original description and the types agree with the NEQ animal, I consider that there was a labelling error during either collection or study of the specimens.

Cooktown is situated in the far north of the Wet Tropics and would have provided ready road access to the area where *H. semoni* occurs. The black form of the animal (Fig. 3a), which was referred to in the original description, comes from the Big Tableland area, near Helenvale, NEQ. The species is placed in *Thularion* gen.nov.

Studies of Australian helicarionid semi-slugs are sparse. Baker (1941) figured the anatomy of a specimen of '*Helicarion*' *leucospira* (Pfeiffer, 1857) and R. Kershaw (1979, 1981, 1983) and Dartnall and R. Kershaw (1978) completed studies on some southeastern Australian species. Most references consist of brief single species descriptions and mentions in faunal checklists. Hence it is not surprising that generic relationships and even species identities are poorly understood. Although a comprehensive revision of the group is clearly required the author has dissected a number of other eastern semi-slug taxa in order to place the following observations in a wider context. I am grateful to Ron C. Kershaw for supplying many personal notes and drawings on eastern semi-slugs. They have facilitated this project.

The following abbreviations are used:-

Q-Queensland, NSW-New South Wales, ZMB-Museum für Naturkunde der Humboldt Universität, Berlin, Germany, QM-Queensland Museum, CMVF-complex mesophyll vine forest. DG-prostate, E-epiphallus, EC-epiphallic caecum, EF-epiphallic flagellum, EP-epipallic pore, G-ovotestis, GD-hermaphroditic duct, GG-

albumen gland, LL-left shell lappet, LML-left mantle lobe, P-penis, PPM-main penital pilaster, PRM-penial retractor muscle, PS-penial sheath, RL-right shell lappet, RML-right mantle lobe, S-spermatheca, SH-shell, SP-spermatophore, SS-spermathecal stalk, UT- uterus, UV- free oviduct, V-vagina, VD-vas deferens, Y-atrium, Z-digestive gland.

SYSTEMATICS

Family Helicarionidae

Thularion gen.nov.

DIAGNOSIS

Shell degenerate with incomplete early whorls and membranous base, depressed, and with reduced whorl numbers. Shell sculpture of fine crowded spirals on the protoconch becoming obsolete on the adult whorls; body whorl with widely spaced, spiral furrows. Animal large with shell lappets prominently united posteriorly; left mantle lobe forming a prominent cephalic shield. Genitalia with epiphallic caecum and flagellum. Penis with sheath, internally with a large lamellate pilaster and pustular wall ornamentation; no verge or papilla present.

ETYMOLOGY

Latin *thule* north; referring to the distribution of the genus in northern Australia.

TYPE SPECIES

Helicarion semoni Martens, 1894; herein designated.

COMPARISONS

Thularion differs most markedly from *Fastosarion* (+*Vercularion*) (type species: *Vitrina superba* (Cox, 1871) by its degenerate, depressed shell which has lower whorl numbers. The external animal characters of *Thularion*, particularly the enlarged shell lappets and mantle lobes, are additional discriminating features. *Parmacochlea* (type species: *Parmacochlea fischeri* Smith, 1884) has an even more reduced shell and greatly enlarged shell lappets and mantle lobes. The penis of *Thularion* is pustulose with a lamellate pilaster apically and no vergic structures. In contrast the penial wall sculpture of *Fastosarion* consists of obliquely arranged, longitudinal pilasters complemented by a large central pilaster and either an apical verge or papilla (R. Kershaw, pers. comm.). *Parmacochlea* has a strongly papillose penis interior with a large central papillose pilaster and a verge.

Thularion semoni (Martens, 1894) comb. nov.
(Figs. 1-7)

Helicarion semoni Martens, 1894, p.87, pl.4, fig.8a-e; Smith 1992, p.244.

Parmacochlea semoni (Martens); Iredale, 1937, p.10.

COMPARATIVE REMARKS

Thularion semoni can be distinguished from *Fastosarion brazieri* (Cox, 1873) (type locality: Mt Bellenden Ker, NEQ) by its depressed, degenerate shell (Fig. 2a-b), lower whorl numbers and enlarged shell lappets which are strongly fused posteriorly (Fig. 5a). *Parmacochlea* spp. are smaller and have a simple, plate-like shell. Anatomically the very long penis with apical pilaster (Fig. 5b,c) immediately differentiates *T. semoni* from other sympatric semi-slugs (Stanisic, unpubl.).

PREVIOUS STUDIES

Martens (1894) compared *T. semoni* with *Peloparion helenae* (Godwin-Austen, 1883) from the Sydney region, NSW, on the basis of overall similarity of *T. semoni* to Godwin-Austen's drawings. However, the Sydney semi-slug is much smaller and is only grossly like the northern species (R. Kershaw, pers. comm.). Iredale (1937) referred *T. semoni* to *Parmacochlea* Smith, 1884, without giving reasons. Presumably the allocation was based on the degenerate nature of the shell. However, although the shell of *T. semoni* is reduced it is not plate-like as in *Parmacochlea* spp. The superficial nature of this conchological similarity is highlighted by major differences in anatomy (external and internal) between *Parmacochlea* and *T. semoni*. Smith (1992) listed the species as incertae sedis and indicated that the type was probably lost.

TYPE LOCALITY

Big Tableland, c. 15k S of Helenvale, NEQ - herein designated.

MATERIAL EXAMINED

LECTOTYPE: ZMB46231, Burnett River (error), Queensland. Collected by R.W. Semon. Height of shell 7.00mm, max. diameter 24.92mm, min. diameter 16.58mm, H/D ratio 0.28, whorls $2\frac{5}{8}$ - herein designated.

PARALECTOTYPE: ZMB46231, 1 specimen, same collection data as lectotype (damaged).

OTHER MATERIAL:NEQ; Lorna Doone, c. 15k SE

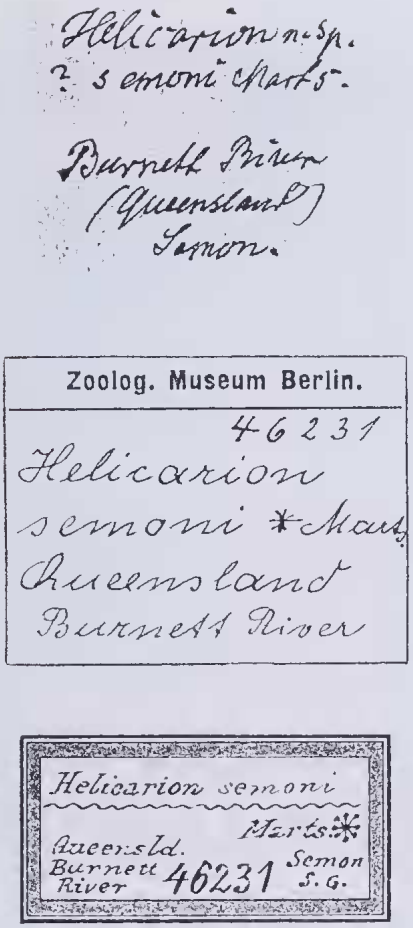

FIG. 1.Provenance of type material

Helenvale, (15°47'S, 145°17'E), CMVF/Palms, under Logs and discarded palm fronds (9, QMMO23769, 4 Oct 1988, J. Stanisic, D. Potter); Mt Finnigan, summit, 1050m (15°48'S, 145°17'E) (4, QMMO44296, 3-5 Dec 1990; 5, QMMO44295 16-17 Jan 1991, G.B. Monteith); Big Tableland, via Helenvale, rainforest, under logs (1, QMMO14166, 17 Dec 1983, J. Covacevich); Mt Misery, via Shiptons Flat (15°53'S, 145°14'E), summit, 850m (1, QMMO44297, 6 Dec 1990, G.B. Monteith); Big Tableland (15°43'S, 145°17'E), 700m (3, QMMO44299, 19-20 Dec 1990, G.B. Monteith); Mt Sorrow, via Cape Tribulation, 300-800m, rainforest (1, QMMO43308, 15 Oct 1980, G.B. Monteith); Table Top, Mt Finnigan, Shipton's Flat, rainforest, in litter (1, QMMO4697, 11 Jun 1971, D. Douglas).

DIAGNOSIS

Shell (Fig. 2a,b) large, maximum diameter 22.00-25.30mm (mean 24.14mm), minimum diameter 16.58-18.82mm (mean 17.49mm), very thin, lenticular, horny, poorly calcified. Whorls 2½+-2⅝+ (mean 2⅝), rapidly expanding. Body whorl greatly inflated and descending slightly in front, with lower margin membranous. Spire and apex flattened. Height of shell 6.49-11.69mm (mean 9.51mm), H/D ratio 0.27-0.53 (mean 0.40). Protoconch (Fig. 4a) of 1¼ whorls, sculptured with fine, crowded, incised spiral lines. Post-nuclear sculpture (Fig. 4c-e) of fine radial growth lines and sparse spiral furrows on the body whorl. Microsculpture (Fig. 4e-f) of very fine, almost obsolete, periostracal, spiral wrinkles. Sutures (Fig. 4b) shallowly impressed. Whorls flattened above and rounded below the periphery. Internal walls of early whorls (Fig. 2b) membranous and incomplete. Lip thin, membranous below. Colour yellow with whitish apex; interior chalky white.

Animal (Figs. 3a,b; 5a) large, body length in preservative 45.9-59.4mm (mean 53.0mm, n=7). Foot moderately broad, tripartite, rounded anteriorly, tapercd posteriorly. Tail relatively long, high, sharply keeled mid-dorsally. Caudal horn vestigial; caudal foss a long vertical slit in the tail. Pedal grooves typically aulacopod. Colour (in life) black and reddish-brown with

FIG. 2. Lectotype of *Thularion semoni* (Martens 1894), ZMB46231. Scale in mm.

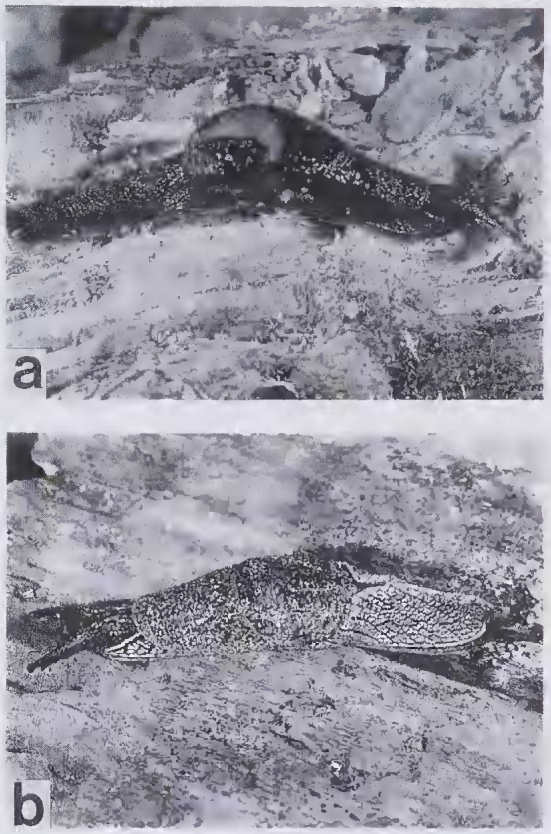

FIG. 3.Colour morphs of *Thulariom semoni*. a, black, Big Tableland, NEQ, QMMO14166; b, brown, Mt Finnegan, NEQ, QMMO4697.

brown markings to black (Fig. 3a,b), always with varying degrees of paler creamy-yellow markings on the body ornamentation; pustules on mantle lobes and shell lappets also with paler markings. Foot black to reddish-brown with paler edges and paler central region. Right mantle lobe small, with short, lobate anterior extension. Left mantle lobe large, with a triangular, tapered lobe posteriorly, expanded into a cephalic shield anteriorly, and fused with left shell lap anteriorly. Right shell lap fused with right mantle lobe at lower margin and with left shell lap posteriorly. In life, right shell lap covering apex and about one-third of shell; left shell lap covering remainder of shell.

Genitalia (Fig. 5b) with multilobate ovotestis buried in the digestive gland. Talon a blind spherical pouch on a short peduncle embedded in the surface of the albumen gland. Hermaphroditic duct long and convoluted; carrefour embedded in the albumen gland. Prostate a band of creamy alveoli appressed to the upper three-quarters of uterus. Uterus with a short, narrow basal section, giving rise to a larger, highly sacculated apical portion. Vas deferens arising from the prostate-uterus as a highly convoluted, thin tube, descending to the penioviducal angle then ascending the penis as a straight narrow tube to enter a wider, muscular epiphallus. Epiphallus shorter than penis, apically with a long thin flagellum which is weakly connected to the side of the penis, internally with longitudinal pilasters basally, becoming transverse apically. Penial retractor muscle inserting sub-apically onto epiphallus at a point where a short, club-shaped caecum arises. Vagina short with irregularly arranged, thin, longitudinal thickenings. Free oviduct expanded, internally with longitudinal thickenings that become transverse apically, entering vagina sub-apically. Spermatheca with a long, thin stalk and an ovately elongate head, inserted apically on vagina. Penis (Figs. 5b,c) long, reflexed centrally; apical region with simple entrance of epiphallus and short, crowded, transversely elongate pustules that become less crowded in some areas and a long, slender, lamellate pilaster; basal region with a sheath, internally with short, narrow, crowded, transverse pustules, tending to be more crowded centrally. Atrium short, without unusual features. Spermathophore (Fig. 5d) elongately ovoid with a long, thin chitinous tail. Based on three (two dissected) specimens (QMMO23769, QMMO14166).

Radula (Fig. 6a-f) having a tricuspid central tooth with lanceolate mesocone and reduced lateral cusps; laterals strongly bicuspid with endocone reduced to a tiny point on the edge of the mesocone, ectocone short and pointed, anterior edge irregularly swollen and grooved; marginals bicuspid with a long curved shaft, long and curved mesocone, short ectocone, no endocone, rounded cusps. Basal plates of central and laterals short, squarish, asymmetrical in laterals with an elevated lateral ridge. Interrow support provided by interlock of anterior edge with basal plate of tooth in front. Radular formula 83.23.1.23.83.

Distribution and Habitat

Tropical rainforests of the coastal region between Cape Tribulation and Cooktown, NEQ (Fig.7); mainly in the uplands and highlands; probably an opportunistic riparian species in the foothills where circumstances allow. Its apparent absence from the Thornton Peak area, south of Cape Tribulation needs confirmation.

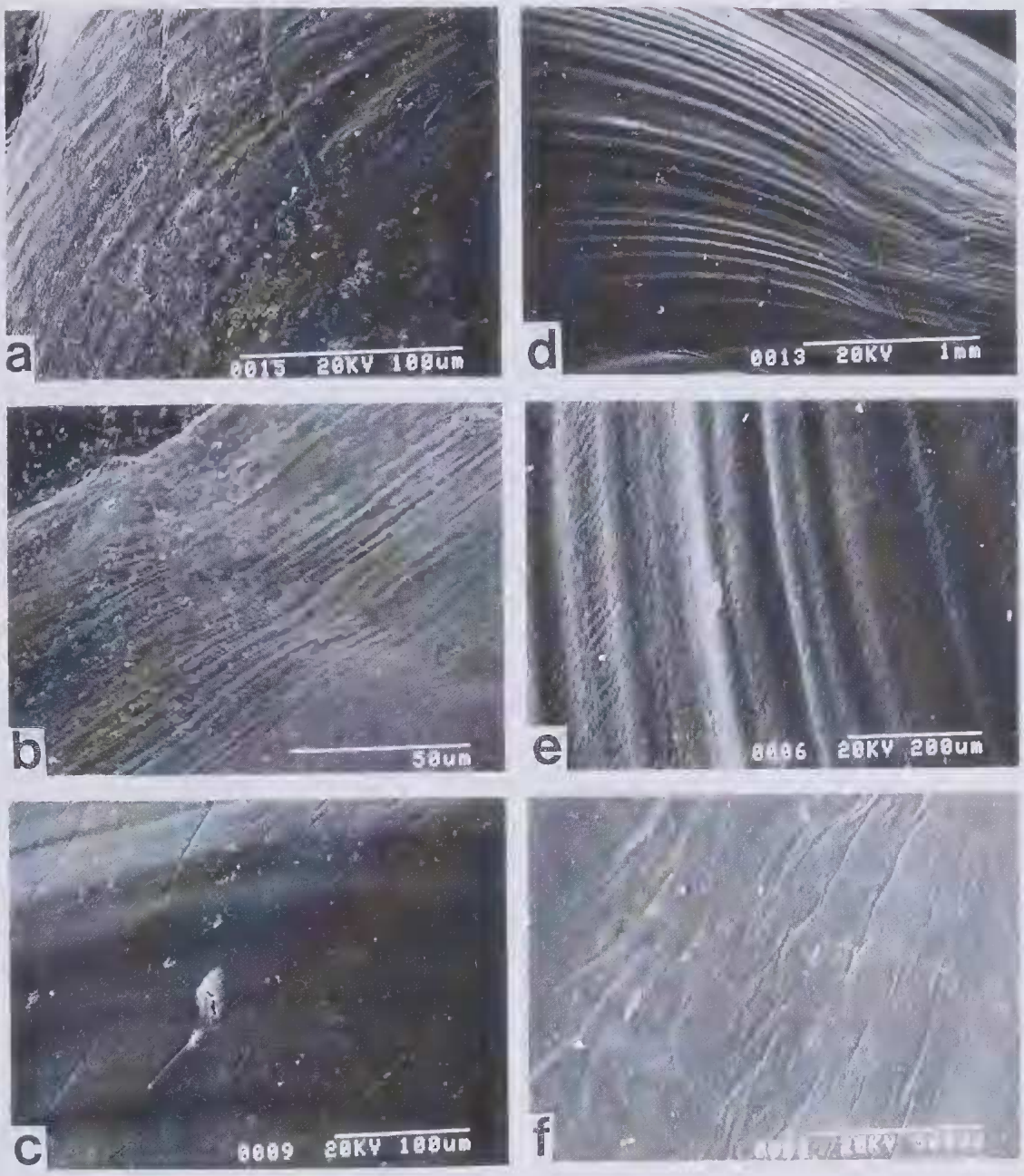

FIG. 4.Shell details of *Thularion semoni*. a-c, Mt Finnegan, NEQ, QMMO44296; d-f, Lorna Doone, NEQ, QMMO23769. a, spiral furrows on body whorl; b, protoconch sculpture; c, periostracal scratches on body whorl; d, radial growth ridges on body whorl; e, microsculpture on body whorl; f, radial periostracal wrinkles due to drying. Scale lines as marked.

REMARKS

Thularion semoni differs from species of *Fastosarion* and *Parmacochlea* in external anatomy, shell features and genitalia and appears to represent a level of semi-slug development intermediate betwecn these two genera. For these reasons it has been given separate generic status.

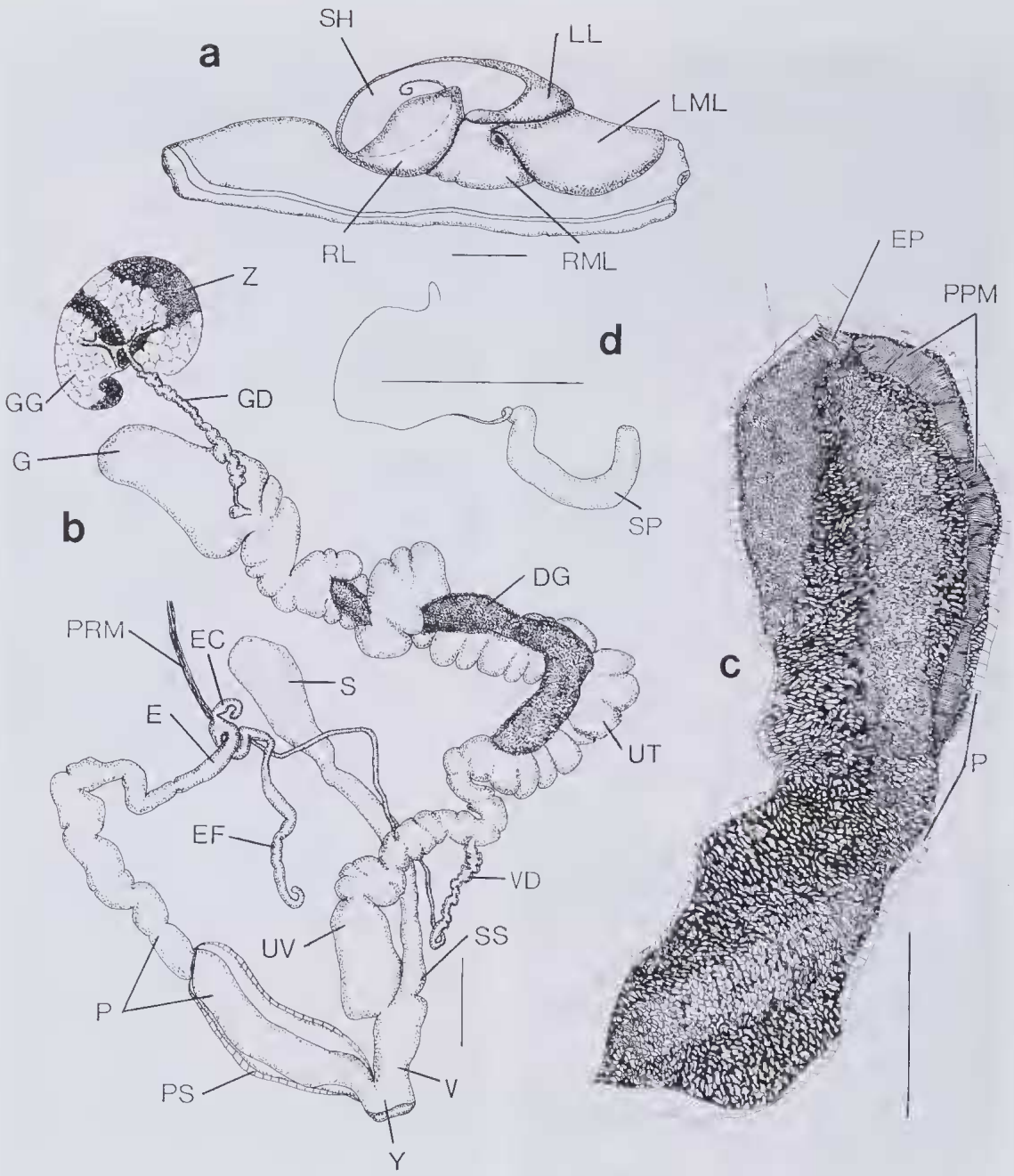

FIG. 5.Anatomy of *Thularion semoni*. a, Big Tableland, NEQ, QMMO14166; b-d, Lorna Doone, NEQ, QMMO23769. a, whole animal showing shell lappets and mantle lobes (body ornamentation not shown); b, reproductive system; c, penis interior; d, spermatophore. Scales lines = 5mm.

DISCUSSION

Establishing the identity of *T. semoni* provided an opportunity to study some features of the east coast semi-slug fauna. Although most species have a superficial similarity this gross resemblance overlays a complex evolutionary history.

Concentration of helicarionid semi-slugs in the coastal and subcoastal mountain ranges of eastern Australia is not accidental. These mountains are mostly volcanic and their eastern slopes lie in the

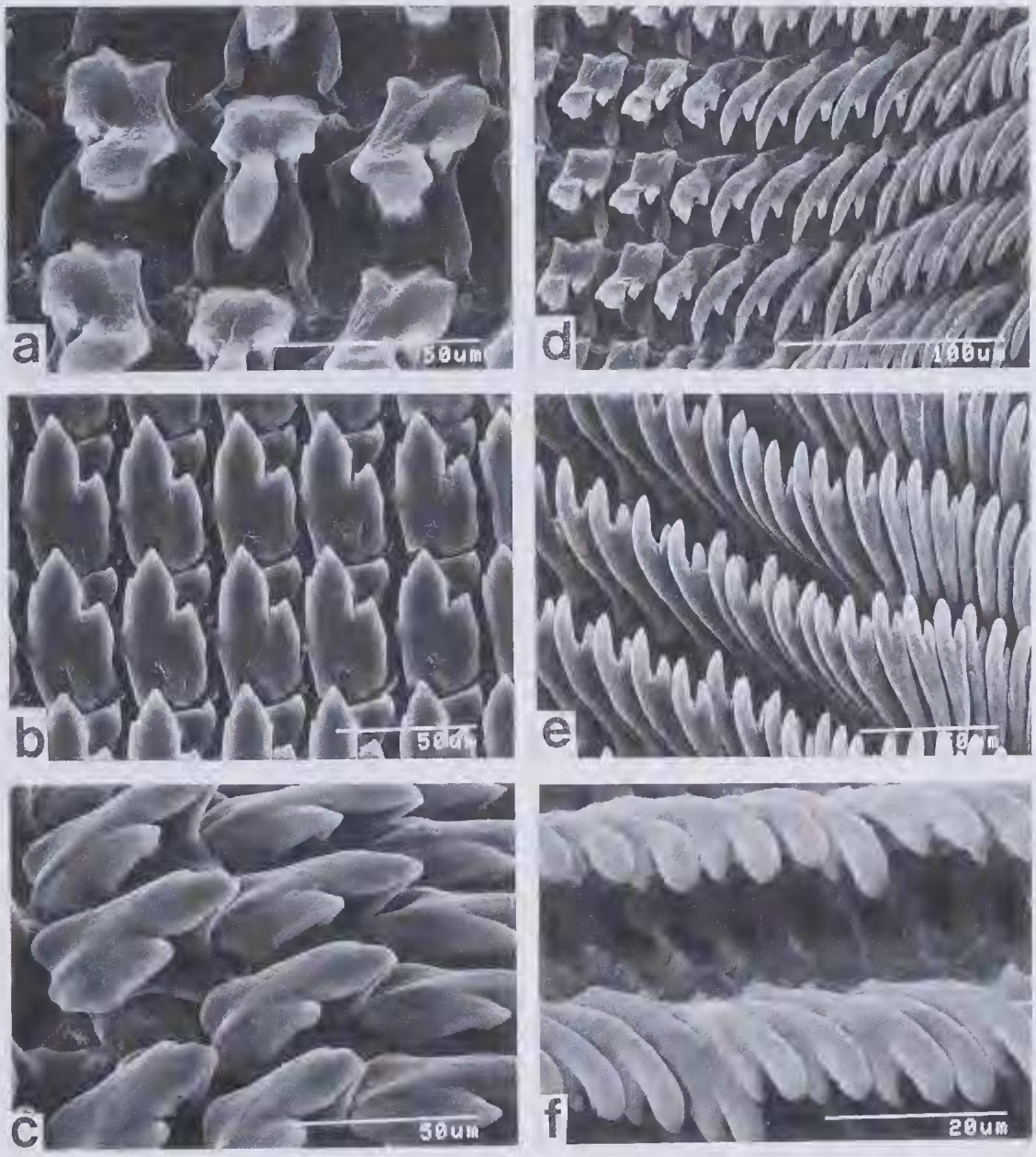

FIG. 6.Radular details of *Thulurion semoni*, Lorna Doone, NEQ, QMMO23769. a, central and lateral teeth showing irregular anterior edge and elevated ridges on basal plates; b, laterals; c, laterals showing interrow support mechanism; d, laterals and marginals; e-f, marginals. Scale lines as marked.

path of prevailing winds which provide plentiful rain. The derived soils are acidic and there is relatively little calcium available for shell manufacture. Under these conditions the need for a shell to resist desiccation is reduced and the energy budget required to produce a shell is increased providing an ideal environment for slug evolution.

The Helicarionidae is considered a recent addition to the Australian land snail fauna having migrated from the Indo-Malayan area following collision of the Australian plate with the Sunda

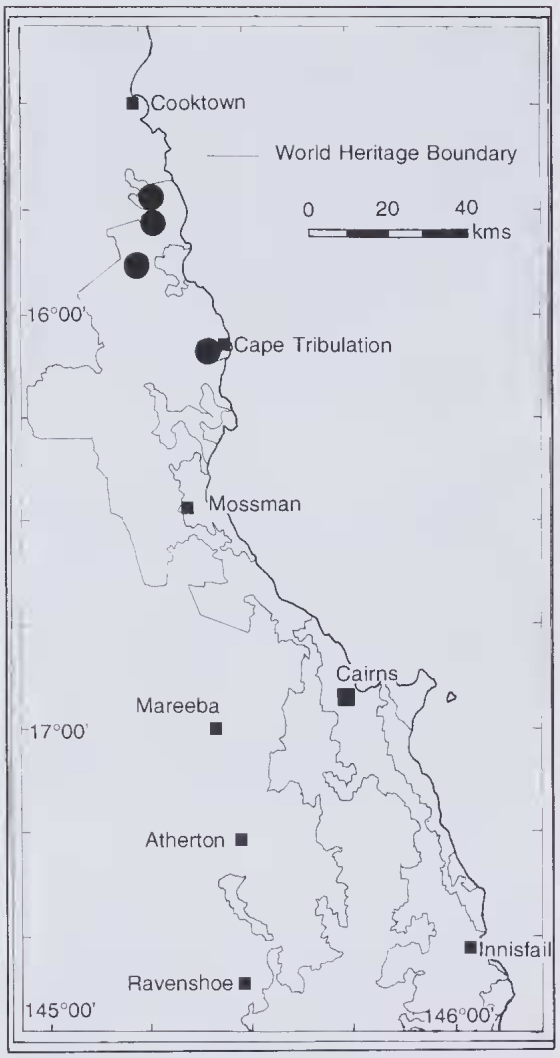

FIG. 7. Distribution of *Thularion semoni* (dots).

Island arc in the mid-Miocene (Bishop, 1981). The post-Miocene drying of the continent, which led to the retreat of mesic habitats elsewhere, would have been ameliorated along the east coast by the presence of elements of the Great Dividing Range. They maintained moist forests along their length and, most likely, provided a corridor for movement and colonisation of semi-slugs in eastern Australia. Drying events of the late Quaternary occurred in more rapid succession than those of the Miocene and Pliocene (Galloway and Kemp, 1981) and would have had severe impacts on moisture-sensitive animals such as semi-slugs. Many groups would have survived only in upland refugia and the present-day distribution patterns of *Mysticarion* (highlands of the Great Dividing Range from SEQ to central NSW) and '*Helicarion*' *australis* in the uplands of the Border Ranges, SEQ (alt>800m), are probable examples of the results of this climatic attrition.

The move to slugdom (limacization) has occurred more than once and probably in more than one way, and in the Wet Tropics region three distinct grades of semi-slug development are evident. These correlate with degrees of shell reduction - least in *Fastosarion* (relatively high whorl count, fully formed whorls, spire elevation) and greatest in *Parmacochlea* (very low whorl count, shell flat and plate-like). *Thularion* with a depressed shell that has a relatively low whorl count, incomplete internal whorls and a membranous base is intermediate between these extremes. Elsewhere along the east coast many semi-slugs e.g. *Helicarion* s.s. show the *Fastosarion* shell form but in the wetter parts of the eastern ranges (Border Ranges, SEQ; New England - Barrington Tops area, NSW; Clarke Range, MEQ) more extreme examples of shell reduction are evident.

The distribution and habitat of *Thularion semoni* indicate that the high mountains of the northern Wet Tropics were probably crucial in its survival, especially during more recent drying events (Kershaw, 1981). Compared with *Fastosarion brazieri*, which has been recorded from many upland (Atherton Tableland) and lowland localities in the Innisfail-Cairns area, *T. semoni* is known almost exclusively from upland and highland localities. The greater shell reduction in *T. semoni* and concommitantly greater area of exposed animal tissue (including expanded shell lappets and mantle lobes) makes this species potentially more sensitive to climatic fluctuation than *F. brazieri*. This provides an ecological basis for explaining not only its current distribution pattern but also past restrictions of the species. The role of montane refugia in Wet Tropics land snail biogeography has been previously highlighted for the Gondwanan family Charopidae (Stanisic, 1987). Their importance to 'modern' families highlights the significant effects of Late Tertiary climatic fluctuations on all east coast terrestrial molluscs.

The relationships of *Thularion* are problematic, due mainly to the lack of adequate revisionary studies on related taxa. The conchological and anatomical features of *Thularion* can be derived from the more generalised *Fastosarion* and it is probable that it is a localised derivative of a *Fastosarion* - like ancestor. Interestingly no *Fas-*

tosarion grade semi-slug is found north of the Daintree R., indicating that *Thularion* may have colonised this region in the absence of *Fastosarion*. The restriction of *T. semoni* to the northern part of the Wet Tropics again exposes the role of the Daintree R. as a possible barrier to land snail dispersal in the region (Stanisic, 1987). Whether or not *Parmacochlea* is a direct descendant of a *Thularion* - like ancestor or whether it is derived independently from a more generalised ancestor has yet to be determined.

ACKNOWLEDGEMENTS

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